

Surficial Shell Resorption in *Nautilus macromphalus* Sowerby, 1849

by

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Abstract. Like many prosobranch gastropods, *Nautilus macromphalus* Sowerby, 1849, resorbs a thin layer of shell material from the surface of its penultimate whorl prior to extending the edge of the black layer during growth. The resorption occurs along a millimeter wide band skirting the edge of the black layer and apparently is accomplished by the mantle edge. The depth of resorption is uneven within and between individuals. This is the first report of shell resorption among the extant Cephalopoda. Surficial resorption in cephalopods must have evolved independently from the gastropods but is postulated to serve a common function in both groups: to provide a fresh surface to which new shell material may be attached.

INTRODUCTION

RESORPTION is a normal component of shell growth in many marine gastropods. In addition to the well-known examples of resorption to remove obstacles to further growth, such as varices on muricid gastropods (CARRIKER, 1972), or to enlarge the shell interior, as occurs in *Conus* (KOHN *et al.*, 1979), more subtle patterns of resorption are common. Many prosobranch gastropods resorb a thin sheet of shell material from the surface of the penultimate whorl (GRAY, 1833; SIGNOR, 1982). The resorption is limited to an area in the parietal region as wide as, or slightly wider than, the shell surface the body whorl will cover after further growth. Surficial resorption removes very little shell material; in *Terebra dimidiata* (Linnaeus, 1758) (Neogastropoda: Terebridae) the total thickness of the resorbed material is only a few micrometers. One hypothesized function of surficial resorption is to provide a fresh surface upon which new shell material can be deposited (SIGNOR, 1982).

If the foregoing hypothesis is correct, one should expect surficial resorption to occur in the other extant group of multiwhorled mollusks with conjoined whorls, the Nautiloidea. In secreting its shell, *Nautilus* must contend with the same constructional problems encountered by gastropods. Both must securely attach new shell material to the surface of the conch without detracting from the shell's structural integrity. Furthermore, because the first nautiloids were cyrtconic, surficial resorption must, if present, have evolved independently from the Gastropoda or

any common ancestor. In this perspective, *Nautilus* is an ideal comparison group for testing the structural integrity hypothesis for the functional significance of surficial resorption.

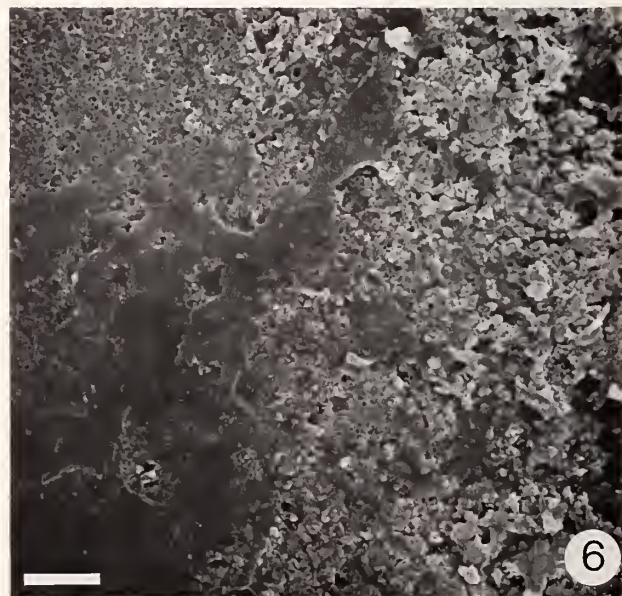
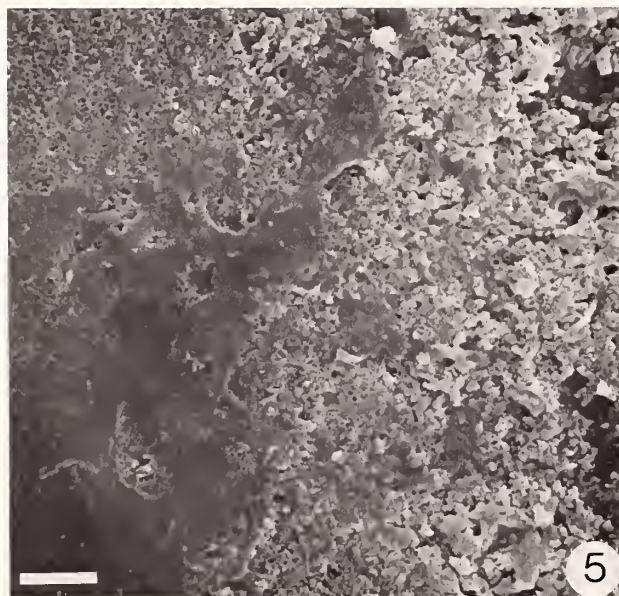
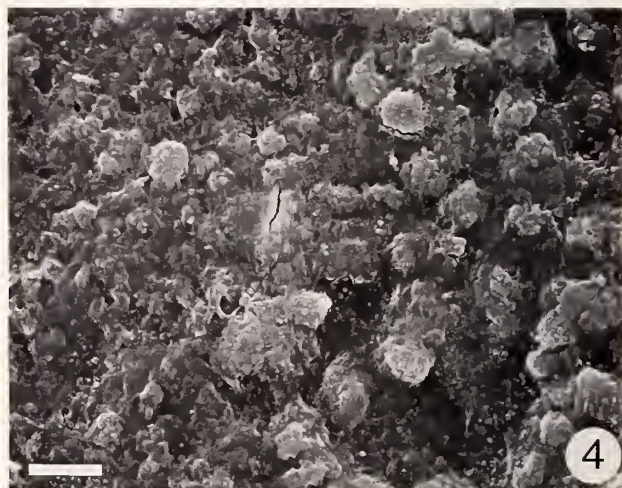
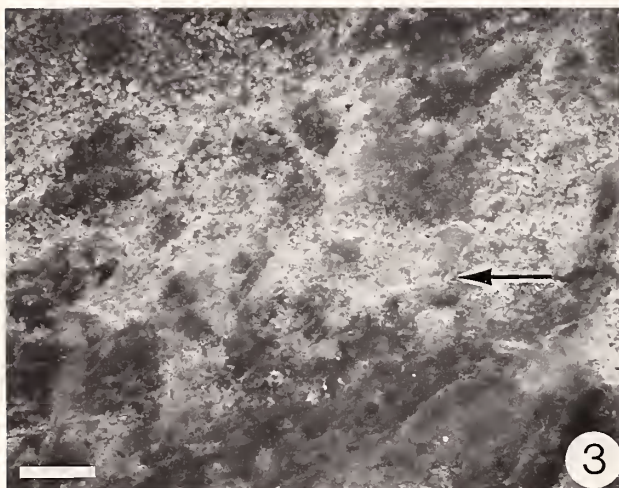
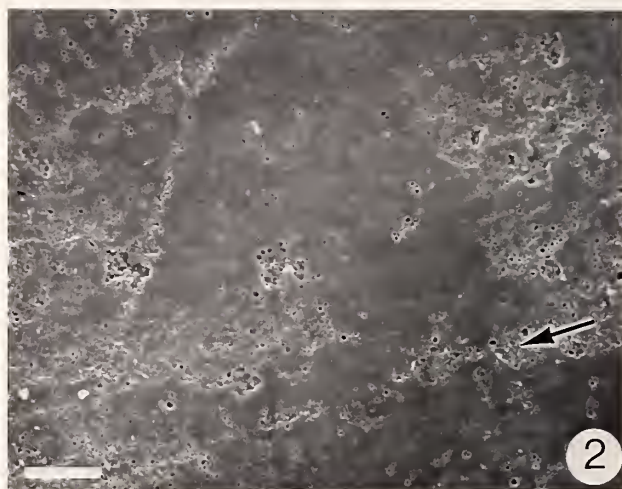
Shell resorption has not been described previously in *Nautilus*, and surficial resorption has not, to my knowledge, been observed among extant Cephalopoda. Shell resorption in the Nautiloidea has been postulated previously (TASNÁDI-KUBACSKA, 1962) but only in the context of decollation of primitive nautiloids.

The *Nautilus* shell is planispiral, involute, and consists of about three whorls in mature specimens (Figure 1). Microstructurally, the outer shell wall is comparatively simple, consisting of three aragonitic layers (BØGGILD, 1930; GRÉGOIRE, 1962; STENZEL, 1964; ERBEN *et al.*, 1969; MUTVEI, 1972). The outer shell layer (often referred to as the porcellaneous layer) is composed of irregular prismatic crystals while the thicker, middle layer is nacreous. The thin inner prismatic layer consists of small prisms oriented perpendicular to the shell surface (ERBEN *et al.*, 1969). The septal microstructure is more complex but is also primarily nacreous (BØGGILD, 1930; GRÉGOIRE, 1962; STENZEL, 1964; ERBEN *et al.*, 1969; MUTVEI, 1972). Growth is determinate (COWEN *et al.*, 1973); the animal ceases to deposit the characteristic irregular color bands in the last half whorl of growth and the final septa are closely approximated.

Nautilus deposits a dull black organic film above the dorsal region of the aperture (Figure 1). The origin of this layer is uncertain but it is apparently deposited by



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the mantle edge (Joubin, 1892; Stenzel, 1964). Once deposited, the black layer remains unbroken until it is covered by nacre. Shell resorption, if present, must occur along the dorsal perimeter of the black layer, where the mantle edge rests during life.

MATERIALS AND OBSERVATIONS

Live specimens of *Nautilus macromphalus* Sowerby, 1849, were collected by Peter D. Ward near Noumea, New Caledonia. The animals were removed from the shells and the clean shells returned to the University of California, Davis, for further study. Only immature specimens were examined in the scanning electron microscopy phase of this study. If surficial resorption exists in *Nautilus* and occurs in conjunction with growth, as in gastropods, there would be no reason to expect evidence of resorption in adults, where growth has ceased. Immature individuals were initially identified by size and color pattern; this characterization was later confirmed by a lack of approximated terminal septae when specimens were sectioned. The specimens were prepared for examination by scanning electron microscopy (SEM) by cutting free centimeter-square size pieces of the shell exterior. Most pieces were cut so as to center the boundary between the black layer and the unmodified surface of the penultimate whorl but other areas of the shell surface were also examined. The specimens were cleaned with ethanol and an ultrasonic bath, mounted on SEM stubs, and then sputter-coated with gold/palladium and examined under SEM.

Visual examination of *Nautilus macromphalus* reveals that the edge of the black layer is usually slightly lower than the unmodified shell surface. (This is often most easily detected by running a fingernail over the boundary between the black layer and the unmodified shell surface.) The degree of offset varies from individual to individual, in some cases appearing flush and in others having the black layer visibly below the unmodified shell surface. The offset cannot reflect the presence of a low growth line, because the edge of the black layer is not congruent with growth lines. The only possible explanation for the black layer lying below the level of the shell surface over

which it is extending is that shell resorption occurs before the advance of the black layer.

Examination of specimens cut perpendicular to the boundary of the black layer shows that the thin outer shell layer, the porcellaneous layer, extends under the black layer. Therefore, resorption cannot remove more than about 0.18 mm of shell material, the approximate thickness of the porcellaneous layer. Measurement of the thickness of the outer shell layer, using an ocular micrometer, shows the portion under the black layer is approximately 0.12 mm, or averages about two-thirds the thickness of the uncovered portion of the outer shell layer. Resorption prior to deposition of the black layer is the only plausible explanation for this reduction in the thickness of the porcellaneous layer.

Under low-power optical magnification the normal shell surface appears vitreous. Along the edge of the black layer the shell surface has a hazy luster, suggesting that some modification of the shell surface has occurred.

Under scanning electron microscopy, the shell surface of *Nautilus macromphalus* has an irregular, pitted appearance (Figure 2). Fine growth lines are visible as uneven cuestas, apparently formed when new growth extends the shell from beneath the previous shell edge. Small pits are scattered unevenly over the surface and are densely concentrated in some areas. These concentrations usually fall along growth lines or where the shell apparently was damaged. The pits can approach one micrometer in size but most are less than half that diameter. The origin of the pits is unknown; one possibility is that they are produced by an endolithic organism, perhaps a boring fungus.

At the edge of the black layer the shell is irregularly eroded to a depth of several micrometers (Figure 3). The erosion occurs only along a band, about 1 mm in width, between the black layer and the unmodified shell surface. The depth of resorption is extremely variable, from a few micrometers up to several hundred micrometers. The eroded area is rough in appearance, with irregular hummocks of shell material separated by more deeply eroded areas (Figure 4). The advancing black layer eventually covers the eroded region and is itself later overgrown by further deposits of nacreous shell material.

Explanation of Figures 1 to 6

Figure 1. Immature *Nautilus macromphalus* from New Caledonia. Photo courtesy of P. Ward. Scale bar is 3.4 cm.

Figure 2. Shell surface of *Nautilus macromphalus*. Illustrated area is from flank of body chamber. Arrow indicates position of small, irregular cuesta interpreted here as growth line. Scale bar is 5 μm .

Figure 3. Boundary between unmodified shell surface and resorbed area on flank of penultimate whorl. Arrow indicates po-

sition of boundary. Direction of growth is to top. Scale bar is 50 μm .

Figure 4. Resorbed area at boundary of black layer. Note uneven, hummocky appearance. Scale bar is 5 μm .

Figures 5 and 6. Stereo pair of the boundary between the resorbed area and the unmodified shell surface. Direction of growth is to the right. Scale bars are 4 μm .

The morphology of the resorbed area is shown in Figures 5 and 6, a stereoscopic pair of micrographs taken of a single specimen. (The two pictures show the same region but are taken from two different angles, 6 degrees apart.) Perceived depth-of-field in SEM images can often be deceiving, because electron shadowing in SEM micrographs is quite different from patterns of illumination normally encountered in the human environment. In Figures 5 and 6, the resorbed area to the right of the micrographs sometimes appears to overlie the unmodified shell surface shown at the left of the picture. When examined through a stereoscopic viewer, it is immediately obvious that resorption has cut down into the shell surface shown at right.

Shell resorption in *Nautilus macromphalus* occurs along the entire margin of the black layer, from umbilicus to umbilicus. No portion of the shell's surface is covered by the black layer before the surface is modified by resorption.

DISCUSSION

Surficial resorption in *Nautilus macromphalus* is generally similar in form to that observed in many prosobranch gastropods, although the precise pattern of resorption differs somewhat in detail. In *N. macromphalus* the resorption is relatively deep and irregular, whereas the shallow, even resorption in the prosobranch *Terebra dimidiata* produces a smooth, flat surface (SIGNOR, 1982). Unlike most prosobranch gastropods, *N. macromphalus* alters the entire surface of the penultimate whorl, less narrow bands at the umbilici, but this reflects differences in shell geometry and not function. Despite these small differences, the effects of the resorption are identical: to remove the surface of the penultimate whorl as growth proceeds.

Surficial resorption is so widespread among different taxa of prosobranch gastropods that it is difficult to imagine resorption serving a function relating to the specific ecology of each given species. The convergent evolution of surficial resorption in *Nautilus macromphalus* greatly strengthens this argument. The ecology of *Nautilus* is very different from any prosobranch gastropod; what *Nautilus* and prosobranch gastropods have in common is a coiled shell where fresh growth surfaces contact and overlie older shell. The function of surficial resorption most likely lies in the few commonalities shared by prosobranch gastropods and *Nautilus*. The hypothesis that the function of surficial resorption is constructional, and that the mantle edge prepares a suitable surface to which the black layer and new shell material can be attached, meets the foregoing criterion. Alternatively, the function, if any, of surficial resorption could be to remove small epibionts or boring micro-organisms which might infest the shell's surface.

Relatively large calcareous epibionts are demonstrably too large to be removed by surficial resorption. Serpulid tubes not removed by the *Nautilus* during growth are simply plastered over by the black layer and, later, by na-

creous deposits (JOUBIN, 1892; STENZEL, 1964). LANDMAN (1983) documents the occurrence of a barnacle that grew on a live, juvenile *Nautilus*. The side of the barnacle was plastered with alternating layers of black organics and aragonite.

Surficial resorption in *Nautilus macromphalus* must be a convergently evolved character, because the most primitive and earliest orders of nautiloids, the Plectronocerida, Ellesmerocerida and others, consist of orthoconic and breviconic forms (SWEET *et al.*, 1964; YOCHELSON *et al.*, 1973; DZIK, 1981; CHEN & TEICHERT, 1983). Since growth in these straight or slightly curved forms would not involve overgrowth or extension of the mantle over previously deposited shell, surficial resorption would not have occurred. Surficial resorption must have appeared later in the evolution of the nautiloids, along with or after the evolution of coiled conchs where successive whorls were in contact with each other.

It would be interesting to determine whether the other great clade of fossil cephalopods, the Ammonoidea, exhibited surficial resorption. Answering this question would require extremely well-preserved fossil specimens. Thus far, I have not been able to obtain sufficiently well-preserved material to allow detection of surficial resorption, if present, in this group.

While resorption of shell material is commonplace among the Gastropoda, to my knowledge this is the first report of shell resorption among the extant Cephalopoda. Resorption may have occurred among extinct cephalopods, however. For example, the decollate nautiloids (*e.g.*, *Sphooceras truncatum* [Barrande, 1868]) might have resorbed a portion of the conch, allowing separation of the deciduous portion (TASNÁDI-KUBACSKA, 1962), in much the same way as the gastropods *Caecum* (BERNER, 1942) or *Rumina decollata* (KAT, 1981) weaken their shells by resorption prior to shedding the deciduous portion. The mechanism by which this resorption, if present, would have occurred is uncertain. Resorption requires direct application of the mantle to the area where shell material is to be removed. Although authors have postulated the presence of "cameral mantle" to account for the formation of cameral deposits in some nautiloids (TEICHERT, 1933, in FISCHER & TEICHERT, 1969; FLOWER, 1939; KOLEBABA, 1974), there is no compelling evidence for the presence of living tissues within the camerae, except the siphuncle, of any nautiloid (for recent reviews of the debate over formation of cameral deposits, see FISCHER, in FISCHER & TEICHERT, 1969; DZIK, 1981; CRICK, 1982). Thus, it is uncertain if resorption did occur in conjunction with decollation in primitive nautiloids and, if so, how that resorption might have occurred.

An important and unresolved question is how gastropods and *Nautilus* accomplish shell resorption, and what happens to shell material secondarily removed by the animal. It is not certain that uptake of ions removed from the shell occurs in the mantle, nor is it certain what part of the mantle might be responsible for the resorption.

Lacking this information, the term "resorption," while well established in the literature for this process, must be applied with caution. Based on current knowledge, it can only be used in the sense of "localized secondary dissolution." The experiments necessary to demonstrate uptake of secondarily dissolved ions through the mantle are tractable, however, and would permit resolution of this question.

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